# ON TROMBELLA ALPHA N.SP. (ACARINA: TROMBELLIDAE) FROM AUSTRALIA: CORRELATION, DESCRIPTION, DEVELOPMENTAL ABNORMALITIES, SYSTEMATICS AND POSSIBLE AUDITORY STRUCTURES

by

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(Manuscript accepted 23 January 1985)

#### ABSTRACT

SOUTHCOTT, R. V. 1986. On Tromhella alpha n.sp. (Acarina: Trombellidae): correlation, description, developmental abnormalities, systematics and possible auditory structures. Rec. 5: Aust. Mus. 19(11): 145-168.

A trombidoid mite (Acarina: Trombellidae) larva, parasitic upon field crickets *Teleogryllus commodus* (Walker) in northern New South Wales, has been reared experimentally to the active deutonymph. The larva, protonymph and deutonymph are described as *Trombella ulpha* n.sp., and the deutonymph compared with previously known species of the genus, particularly *T. warregensis* Hirst and *T. adelaideae* Womersley from Australia.

One reared nymph of *T. alpha* had gross developmental abnormalities of the legs, with shortening or even loss of segments, and nondevelopment of setae, here termed brachymely. Similar occurrences in this and other mites are instanced.

A correlation and a principal component analysis was made of the larval dimensional variates, using various dorsal scutum, leg segmental, and body setae measurements. Three principal components were defined, each including one or more idiosomal variates and one or more leg variates.

A key is presented for the known adults and deutonymphs of *Trombella* of the world.

Leg chaetotaxy of *Trombella alpha*, the only described larva of *Trombella*, is discussed.

The family Trombellidae and its subfamilies Chyzeriinae and Trombellinae are redefined. Generic classification of the Trombellidae is revised. A new genus is erected for adults and nymphs: *Maiputrombella* n. gen., with type species *M. americanum* (Robaux, 1968) its only member, from South America, Keys are provided to the genera of both larvae and of adults and deutonymphs. *Womersleyia* Radford, 1946 is restored to full generic status.

The adult genus *Parachyzeria* Hirst is removed from the family and placed in the Johnstonianidae, as is also the larval genus *Ralphaudyna* Vercammen-Grandjean *et al.* (1974).

The possible functions of some of the structural peculiarities of *Trombella alpha* larva are discussed in relation to existing knowledge and suggestions that have been made for some other prostigmatic mites. The attenuation of the larval tarsi is believed to be related to its function as a sound receptor, serving as a sonar device for the location of the sound-emitting cricket hosts. This suggestion is supported by a significant bias (over 3:1) in the numbers of mites obtained from vocalizing male crickets as against the silent females and because this bias was not found in the sub-adult (i.e. non-stridulating) male instars.

# INTRODUCTION

Berlese (1887) proposed the genus *Trombella* for *T. glandulosa* Berlese, 1887 from northern Italy; a species since recorded from Austria (Schuster, 1960). Originally Berlese gave a definition and description only of the type species, i.e. by referring to the sixteen dorsal depressions. In 1888 he added the South American *T. nothroides* Berl, 1888, which lacks the rounded dorsal opisthosomal depressions.

Womersley (1954b) reviewed the subfamily Trombellinae Thor, 1935 and erected the genus Nothrotrombidium for Trombella otiorum Berlese, 1902, from Europe (see Feider 1955, p. 68; 1958, p. 265), thereby restricting Berlese's genus; he placed in it also T. nothroides Berlese, and T. lundbladi Willmann, 1939 from Madeira (North Atlantic region). Additional species include Nothrotrombidium bulbiferum (Willmann, 1940) (noin. emend.), from Europe and Nothrotrombidium brevitarsum André, 1960 (nom. emend.) (1960a) from Tonkin, Indochina. Trombella s. str. has currently five described species: T. glandulosa Berlese (type), T. warregensis Hirst, 1929 (Australia), T. adelaideae Womersley, 1939 (Australia), T. favosa André, 1936 (1936a) (Africa) and T. lusitanica André, 1944 (Europe).

Genera now placed in the family Trombellidae include Trombella Berlese, Parachyzeria Hirst, 1926 (however, see further below), Parathrombella André, 1958, Neonothrothrombidium Robaux, 1968, based purely on the adult forms, Chyzeria Canestrini, 1897 and Nothrotrombidium Womersley, 1954, known from the adult and the larva, Audyana Womersley, 1954 (1954a) and Durenia Vercammen-Grandjean, 1955, known from the larva and deutonymph, and Womersleyia Radford, 1946, Ralphaudyna Vercammen-Grandjean et al., 1974, and Nothrotrombicula Dumbleton, 1947, known only from the larva.

I reported that larval trombidioid mites, parasitic upon field crickets, Teleogryllus commodus (Walker), in northern New South Wales, and classifiable to Womerslevia Radford, had been reared experimentally to the nymphal stage, and that these nymphs were classifiable as Trombella (Southcott, 1982). It was thus proposed that Womerslevia Radford is a junior synonym of Troinbella Berlese. Previously it was known only from its type species, W. minuta Radford, 1946, a larva taken either free-living from mud, or parasitic under the wings of grasshoppers (Acridoidea: Tetrigidae and Tettigoniidae) on the Island of Gan, Addu Attoll, Maldive Islands; original specimens taken on 20.xii.1944. (A paratype slide in the South Australian Museum collection is labelled (in the writing of one of Womersley's technical assistants) "ex Grasshopper/ Maldive Is/13. Jan 1945 C.D.R." This slide bears also a label in pencil showing that it was used by Vercammen-Grandjean in 1970 in his revision (1972) of the species. 1 have added an identifying number ACB731 to each label.)

This paper describes the larva, protonymph and deutonymph instars of the New South Wales species of *Trombella*, details of the experimental correlation and its taxonomic significance.

The reared deutonymphs appeared to be morphologically similar to the adult Trombella adelaideae Womersley, 1939, known from a single specimen collected "from under a stone at Burnside", in the Adelaide district, South Australia, in August. However, there are differences. One other Australian species is known, based also on a single specimen; this is T. warregensis Hirst, 1929, found "under a log on the bank" of the River Warrego, 4 miles west of Barringun, New South Wales, in August 1928 by Hirst. The total number of species of Trombella in Australia is conjectural, as these mites have been collected and surveyed very inadequately. 1 have seen several as yet undescribed species of larvae referable to Trombella s. str. parasitic upon grasshoppers, whilst surveying the mite ectoparasites of grasshoppers in the Australian National Insect Collection, CSIRO Division of Entomology, Canberra. In view of the uncertainties of attempting to correlate deutonymphal and adult trombidioid (and other prostigmatic) mites on morphological features, it is considered wisest to erect a new taxon, Trombella alpha n. sp., for this species.

After again studying the characters of *Trombella* alpha and other larvae known in the family, *Womersleyia* is restored to full generic status (see further below).

All measurements are given in micrometres ( $\mu$ m) unless otherwise stated.

# Genus Trombella Berlese

#### Synonymy

Note: I have not attempted in the synonymic list for *Trombella* below to define where it covered also

Nothrotrombidium Womersley, 1954. All authors used the genus name of *Trombella* for all species here considered until Womersley's action. It may therefore be taken that from 1887 to 28 May 1954 (the date of publication of Womersley, 1954b) all usages of *Trombella* included, or implied the inclusion of, *Nothrotrombidium*. Subsequently, the great majority of authors used this separation, exceptions being Feider (1955, 1959a), Daniel (1959) and Krantz (1978), who still included *T. otiornm* Berlese, 1902. These remarks apply also to the incorrect spelling as *Thrombella* by some authors. Feider subsequently (1958) became aware of, and accepted, the use of *Nothrotrombidium*.

*Trombella* Berlese 1887, fasc. 40. no. 2; 1888, p. 180; 1893, pp. 91-92, 96, 138, 149; 1894, fasc. 72, no. 6; 1902, p. 127; 1912, pp. 2, 4, 8, 9, 11, 14-16, 18, 22-30. Hirst, 1929, p. 168; Vitzthum, 1929, pp. vii, 63; 1931, 3(11), p. 146; 1940, pp. 144, 145; 1941, pp. 506, 826. Womersley 1934, pp. 181, 185; 1937, pp. 75, 76; 1939, p. 149; 1954b, p. 125. Thor 1935, p. 108. Willmann 1939, p. 15; 1940, p. 215; 1941, p. 59. Thor and Willmann 1947, p. 199. Baker and Wharton 1952, p. 250. Feider, 1950, p. 4; 1955, pp. 26, 41, 68; 1958, p. 265; 1959b, p. 541. Vercammen-Grandjean 1955, pp. 253, 260; 1973, p. 109. Vercammen-Grandjean and Kolebinova 1968, p. 250. Schuster 1960, p. 5. Krantz 1978, pp. 278, 351. Southcott 1982, pp. 286, 290.

*Thrombella* André 1934, p. 472; 1936a, p. 9; 1936b, p. 325; 1938a, p. 215; 1944, p. 230; 1958, pp. 14, 15; 1962, p. 63. Robaux 1967, pp. 3, 4, 7, 109; 1968, p. 453 (incorrect spelling).

#### Trombella alpha n. sp.

Description of holotype larva (specimen ACB7I3A; also supplemented from other specimens) (Figs. 1A, B, 2, 3, 4A, C, 5A, B).

Colour in life orange. Length of idiosoma (partially engorged specimen, slide-mounted) 355, width 215; total length of animal from tip of chelicerae to posterior pole of idiosoma 445.

Dorsal scutum trapezoidal, with a broad projecting anterior "nasus"; anterolateral angles ("shoulders") rounded, obtuse-angled; posterolateral angles evenly rounded. Anterolateral margins indented, lateral and posterior margins concave. Scutal sensilla placed towards rear of scutum, well separated, and closer to level of PLs than ALs with only a faint indication of sctules (branches, see Goff *et al.* 1982) with phasecontrast oil immersion microscopy.

Scutal scobalae (non-sensillary setae) six in number, with two AM setae at about middle of "nasus", the ALs and PLs towards their respective angles; these setae ciliate, slender, tapering, a little blunted, with a single large terminal setulc in many instances.

Standard data of the holotype and a series of other larvae are summarized in Table 1. Raw data are held on file at the South Australian Museum.

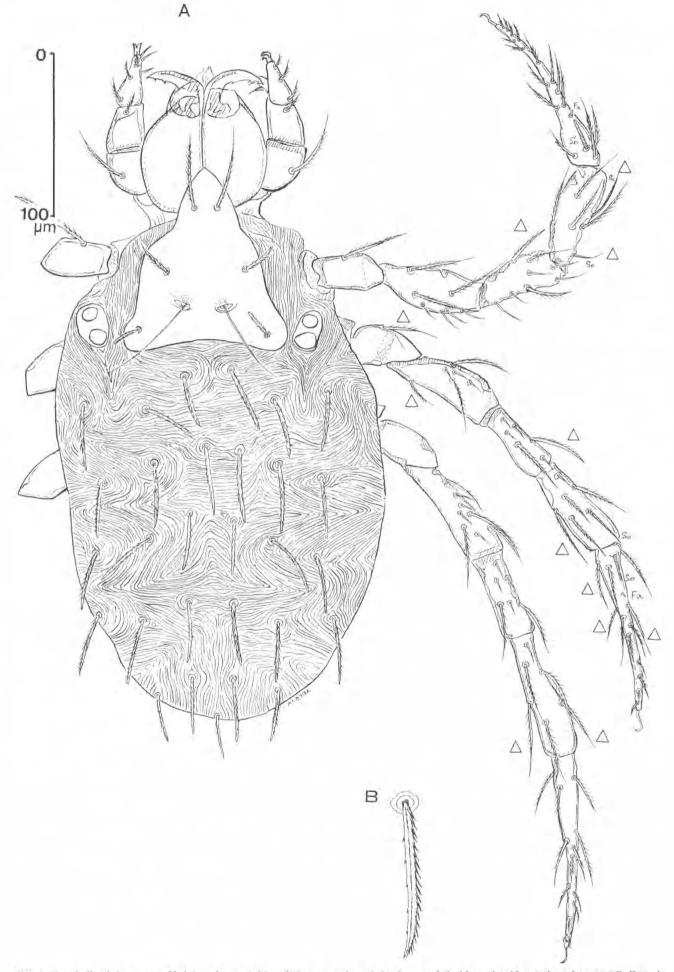


FIG. 1. Trombella alpha sp. nov. Holotype larva. A Dorsal view, to scale on left. (Legs on left side omitted beyond trochanters.) B. Dorsal idiosomal seta, further enlarged (not to scale). In this and in subsequent figures the △ sign indicates the seta is shown in both the dorsal and ventral figures.

June, 1986.

TABLE I, STANDARD DATA AND OTHER MORPHOMITRIC DATA OF A SERIES OF LARVAE OF *TROMBELLA* ALPHA N. SP.

		rements in microm		a 24	-
Character	Holoispe	Range	Mean	5.0-	n
AW	55	55-64	56,67	2.84	12
PW	84	76-90	84.517	4,19	12
SB	25	22-28	24,25	1.60	12
ASB	81	58-81	72.11	9.02	- 9
PSB	34	25-40	35,42	4.60	12
1	120	87-120	108.33	11.27	- 9
W	109	100-118	105.67	5.14	12
AP	-43	34-44	39.00	3.44	11
AN	-46	36-0349	44.78	4.09	9
AL	27	20 = -34	24.55	3.96	11
PL	71	ca18-27	21.30	2.58	10
AMB	32	18 22	19,70	1.66	-10
Sens	-	40-51	43.67	100	3
DS-	39-46	(31-42)-(35-49)	-15.64%	2.16	11
IORI-DS	40-46	(33-42)-(44-49)		-	11
PDS	39-42	(31-37)-(36-48)		1000	-10
Gel	55	51-60	54,83	2,98	12
101	73	62-73	66.33	3.47	12
Gelt	51	47-55	51.00	2.13	12
Till	67	57-69	62.50	1.37	11
GeIII	60	51-60	55.42	2.23	12
THH	87	73-87	79.83	4.39	12

\* For maximum values of DS.

At times setae are broken in the specimens. As Table 1 indicates, it is unusual to find the scutal sensillary setae intact in a mounted specimen. During the moulting process, scutal scobalae commonly fracture. A number of specimens measured here have been allowed to moult. This often results in disruption of the skin, or its crumpling and folding and usually increases the difficulties of measuring. In some cases, however, e.g., in the cast dorsal scutum, it may result in a flattening and better display of the more anterior parts of the scutum, as well as better estimates of the rectilinear length. In fully or partially fed specimens, of the larvae the shield is often, in its anterior part, too curved and obscured for accurate measurements on the slide, and in such cases estimates of L and ASB tend to be unreliable.

Eyes 2+2, sessile, each lateral pair on a distinct ocular plate near PL angle of scutum. Corneae oval, anterior with longest diameter 13, posterior with longest diameter 17,

Dorsal idiosomalae slender, ciliate, blunt-ended, arising from the usual small plates or annuli set in the epicuticle; in rows arranged 6, 6, 6, 6, 4, 1; total 29.

Venter of idiosoma with a pair of scobalae in area between coxae II and III, slender, tapering, pointed, ciliate, 41 long. Behind the level of coxae III and about 38 setae, tapering, ciliate, pointed or slightly blunted, in irregular transverse rows across the opisthosoma, 25-35 long. Anus (uroporus *auct.*), of two longitudinal valves (obscured in holotype; 36 long in ACB712E).

Coxalae 2, 1, 1, normal, pointed, with long setules. Medial coxala 1 placed over about the mid-point of the anterior coxal border, or a little medial to it, 54 long; lateral coxala 1 placed well laterally, over the beavily chitinized anterolateral rim of the coxa, 51 long. Coxala II placed towards outer part of coxa, about 1/3 back from the anterior border, 47 long. Coxala III placed over anterior border, about 1/5 back from its heavily chitinized and projecting lateral part; 46 long.

Leg segmental formula 6, 6, 6, Legs slender, segments from femur to tibia more or less cylindrical; tarsi tapering, attenuated, Leg I 430 long, II 415, III 455 (each including coxa and claw). Pedocoxal supracoxalae not identified, presumably absent.

Tarsus I 116 long, by 18 high at its thickest part, near its origin, Til/Gel = 1.33. Tarsus II 118 by 18; Till/GeII = 1.31. Tarsus III 124 by 18; TillI/GeIII = 1.45. (Tarsal measurements exclude claw and pedicle.) For other leg metric data, see Table 1. One falciform, slender claw to each tarsus.

Leg scobalae (i.e. branched, barbed setae) slender, tapering, pointed, the setules (barbs) moderately outstanding. Leg scobalar formula: trochanters 1, 11, 111 1(1), 1(1), 1(1), femora 6-7(5-7), 7(6-7), 6(6), genua 4(4), 4(4-5), 4(4), tibiae 7(6-9), 6(6-7), 7(7) (figures given for holotype, followed by the range observed in at least six specimens, in brackets).

Femora, genua, tibiae and tarsi with specialized setae (see Figs 1A, 2). Large striate solenoidalae are present on leg segments as figured. In addition to these easily identifiable setae, the femora, genua and tibiae carry small, slender, pointed, smooth i.e. unbranched setae, not optically active. In previous papers 1 have identified these setae by the name of "spinalae". These setae will be referred to here as spinofemoralae, spinogenualae etc., according to my previous system of nomenclature (Southcott 1961a, 1961b, 1963; see also the further comments below). Solenotarsalae 1, 1, 0, Solenotibialae 2(?1), 2(?1), 1(?0) (there is some difficulty in differentiating the more slender of these setae from spinalae). (A previous statement (Southcott 1982, p. 317) that the formula for the solenotibialae in Chyzeria is 0, 0, 0 was wrong, it should be 2, 2, 1 as shown in the figures to that article.) Vestigiotibialae 1, 0, 0. Vestigiogenualae 1, 1, 0.

Guathosoma small, compact, the combined chelae bases from above almost hemispherical; gnathosoma 95 long to front of cheliceral blades, by 82 wide. Cheliceral blades large, transverse, each with three (range 0-3) retrorse teeth along posterior edge. Anterior hypostomala pointed, ciliate, 22 long. Palpal coxala present, tapering, pointed, ciliate, 36 long, Palpal formula 1, 0, 2, 1, 3, 8 or 9. Dorsal palpfemorala tapering, ciliate, 35 long, ventral similar but more slender, 35 long. Palpgenuala tapering, ciliate, placed dorsolaterally, 31 long (from ACB711C; broken in Holotype). Palpal tibialae and tarsalae as figured. Palpal tibial claw bifid, with the tines short, curved, pointed, a little separated, slightly unequal. Palpal supracoxala not identified. Galeala absent.

#### Analysis of the Larval Variates

In an analysis of the data in Table 1, J have eliminated the Sens figures, since only three are recorded. Also, as the data for the various estimates

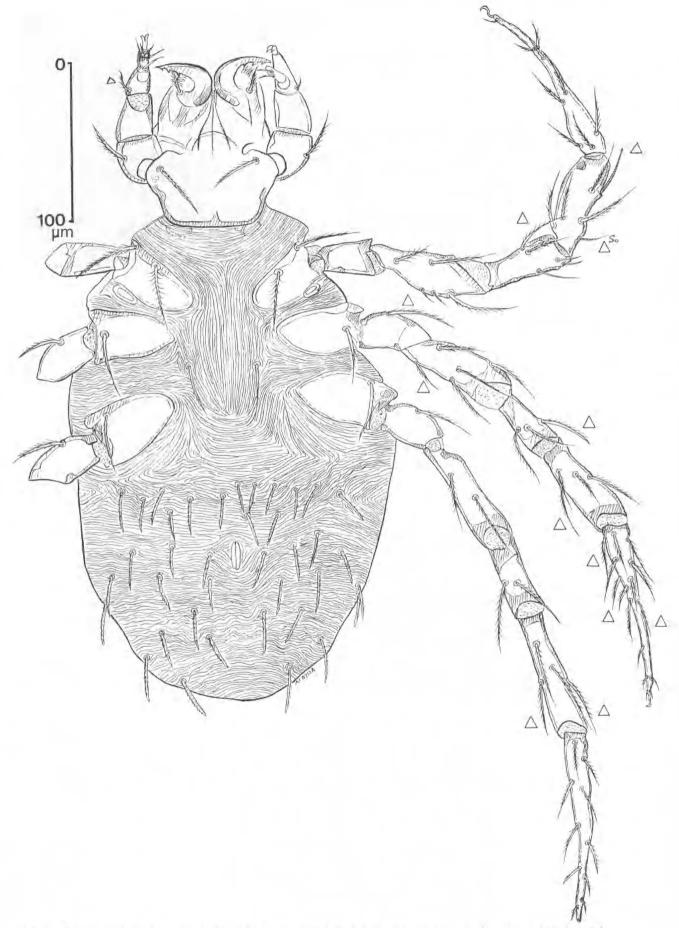


FIG. 2. Trombella alpha sp. nov. Holotype larva. Ventral view (legs on left side of drawing omitted beyond trochanters).

for DS are to some extent redundant, these figures have been restricted to the maximum of the DS. The data are thus reduced to a  $19 \times 12$  table of variates.

A correlation matrix was first calculated from these figures, followed by a principal component analysis (Hotelling 1933). In view of the small number of mites only the first three (independent) patterns are considered.

Pattern 1: The variates ASB, L, A-P and TiIII (and to a less extent TiII and GeIII) varied in the same way, and accounted for about 40% of the patterning. These variates refer mainly to estimates of shield length, together with that for Tibia III.

Pattern 2: The variates AW, PW, PSB, AM and Gel vary together and account for about 30% of the patterning. These refer mainly to shield width estimates, plus Gel.

Pattern 3: The variates DS and Til vary together and make up about 20% of the patterning. This pattern refers only to estimates of the maximum length of the dorsal idiosomal setae and of Tibia I, and has no shield variate component.

It is interesting that there is in each component a representation of a leg variate. It may be commented that these findings appear to differ from results commonly obtained from morphometric studies upon, for example, vertebrates, where the first pattern is usually of a size variable. If such were the case here one would expect that all shield measurements would tend to be represented in Pattern 1. The results could be, to some extent, an indication of the uniformity of the parasite samples available for study.

# Description of Protonymph (see pp. 160-161)

#### Description of Deutonymph

(Figs 6, 7A, B, 8A, B; see also Figs 4C, D, 7C, D) Description based mainly on reared specimen ACB712B.

Colour in life orange. Idiosoma slender, cordate, flattened dorsally, with prominent division between propodosoma and metapodosoma. Propodosoma more or less conical, with base considerably narrower at junction with metapodosoma. Anterior edge of metapodosoma more or less straight, terminating laterally in slightly obtuse but rounded shoulders, continuing into the posterolateral and posterior margins. (In the unfed and unmounted newly emerged nymph the posterolateral borders are somewhat concave; see Fig. 4D). Length of idiosoma from tip of "nasus" to posterior pole 840, greatest width 425, length of propodosoma 200, of metapodosoma 640.

Propodosoma with a pair of dorsal sensillary areas, each sensillum being mounted in a small boss carrying chitinous projections with pointed tips, the whole appearance burr-like. Each boss laterally with a pair FIG. 3. Trombella ulpha sp. nov, Larva in situ, parasitic on a cricket. (SEM by courtesy of M1 S. J. Davidson.)

of short, blunted, ciliate setae, 12, 15 long; each of these setae projecting from individual papillae. Anteriorly, propodosoma produced into a short blunted point overlying cheliceral fangs; from this point the border runs back posterolaterally and almost transversely to an obtuse shoulder, and then more posteriorad.

Anterior and peripheral part of dorsal surface of propodosoma with almost smooth "tear drop" setae, each mounted on an individual papilla, an enlarged and heightened annulus of the seta. Long axis of scobillum of each seta lies more or less transversely upon seta shaft, pointing slightly upwards. The more anterior of these on propodosoma point more or less medially; those on anterolateral parts of dorsum of propodosoma point more or less anteriorly (Fig. 7A).

The more central and posterior part of propodosoma rugose and devoid of setae, the anterior portion, lying between the sensilla, being level, the posterior portion formed into two large projecting bosses, with burr-like projections of epicuticle; propodosoma bordered by "tear drop" scobalae, and, more laterally, more attenuated setae.

Eyes 2+2, sessile, lateral upon propodosoma, lateral and somewhat posterior to sensilla. Each pair consists of an anterolateral and a posterolateral eye, with a thick cornea, each about 16 across.

A single filiform sensillary seta, 96 long, emerges from each sensillary boss.

Hysterosoma dorsally with 16 oval or circular shallow pits in two lateral lines, each of six depressions, and a median longitudinal row of four. Depressions fairly close to each other, and collectively occupy a considerable proportion of dorsum of hysterosoma. Anteromost pit of median row elliptical, somewhat posterior to two anteromost pits of lateral rows; behind it are two circular pits, then an elliptical pit, set among the six most posterior of the lateral pits of the dorsum.

Each pit of lateral row somewhat elliptical or ovoid, second the largest, posteriorad they become progressively smaller.



TROMBELLA ALPHA N.SP.

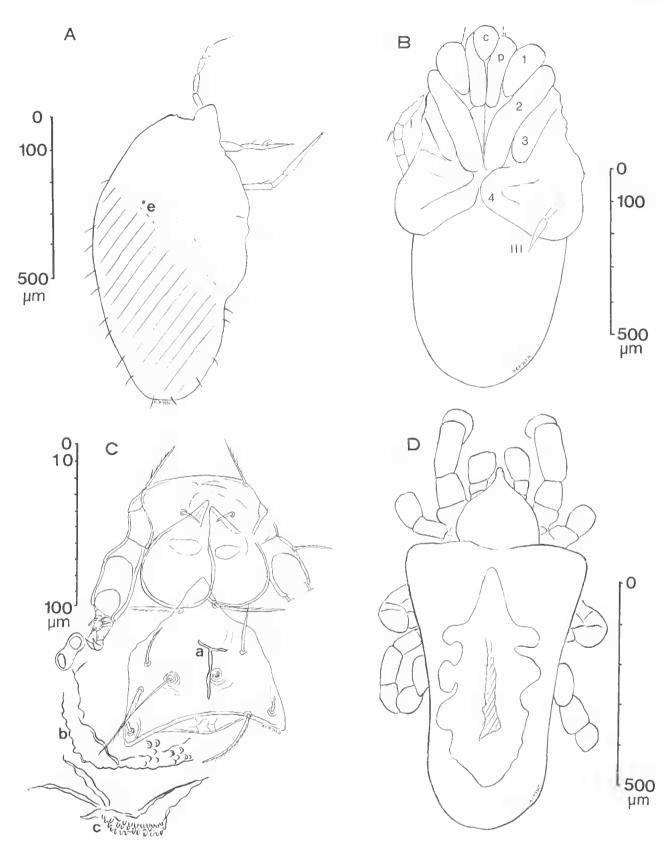


FIG. 4. *Trombella alpha* sp. nov. A Larva in oblique lateral view, undergoing transformation to nymph, specimen ACB712C on 9.iv.1980. *e* eyespot. B Later stage in the larva to nymph transformation, from below, from specimen ACB712B on 9.iv.1980. The nymph is developing within the uncast larval skin, two of the larval legs being shown; fII indicates larval leg III. In the nymph *c* indicates the developing chelicerae, *p* the palpi, and 1, 2, 3, 4 indicate the developing nymphal legs. C Cast larval skin and some of the protonymphal skin (latter drawn in heavier line) (specimen ACB712D). The palpi and basis of the gnathosoma are laid back and these parts of the mouthparts are seen in ventral view. *a* the "Y" or "T"-structure of the deutonymphal skin. *b* another part of the deutonymphal skin. *c* the "mateola" or studded boss of the deutonymphal skin. D Deutonymph (ACB712C) seen in transparency. (All to nearest scale).

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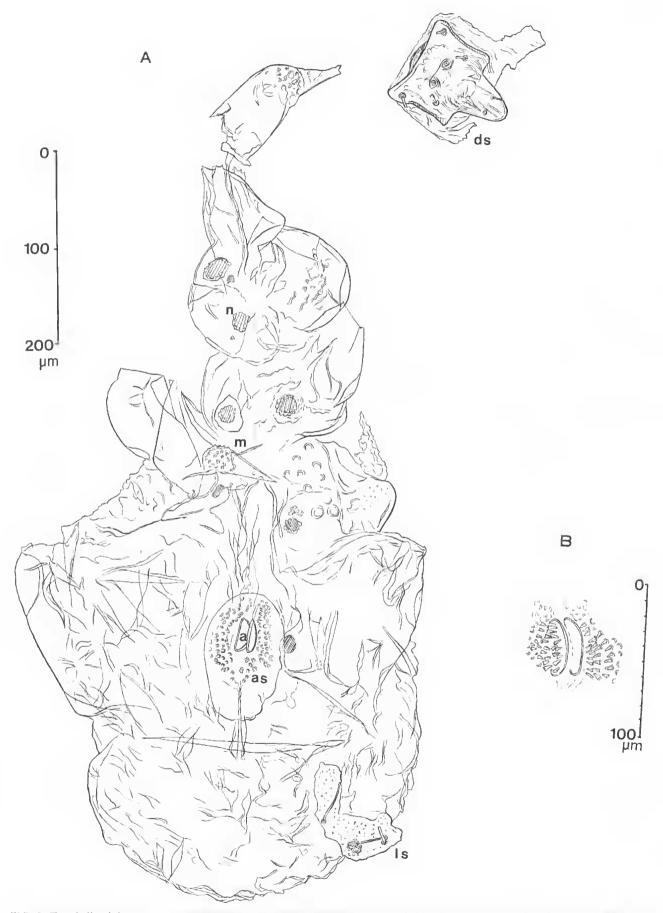


FIG. 5. Trombella alpha sp. nov., protonymph. A An almost intact protonymphal skin, from specimen ACB712A. a anal valves from the larva, as area setosa, m mateola or studded boss, n one of the nodular bodies inside the skin (shown cross-hatched), is attached piece of idiosomal skin of larva, ds dorsal seutum of larva in a fragment of larval skin (to scale on left). B Anal valves and area setosa of another specimen (ACB714B) (to scale on right).

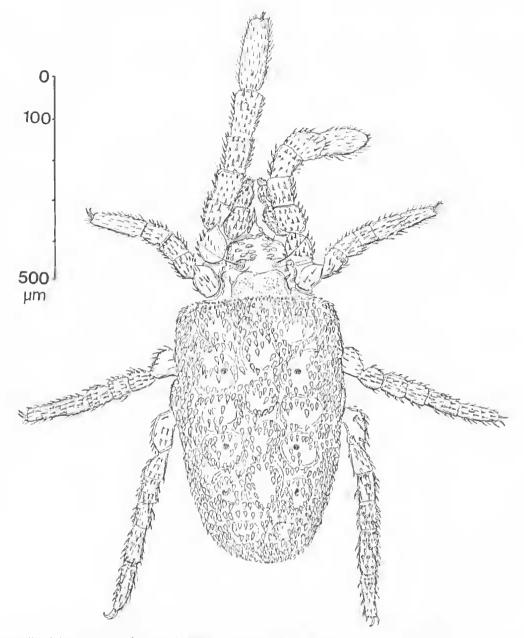


FIG. 6. Trombella alpha sp. nov. Active nymph (deutonymph), specimen ACB712B, dorsal view, entire.

Most of dorsum of hysterosoma densely covered with robust setae, with tear-drop shaped scobillum perched transversely on chitinized "papilla" (seta annulus). Surface of scobillum with faint more or less oblique pattern, visible at high magnification, but scobillar surface smooth in lateral view. These setae occur over most of dorsum, including pits, but are sparser in inner parts of pits. Setae smaller in anterior part of dorsum of metapodosoma, and surfaces tend to project, thus resembling small burrs; laterally setae tend to elongate and be ciliatc.

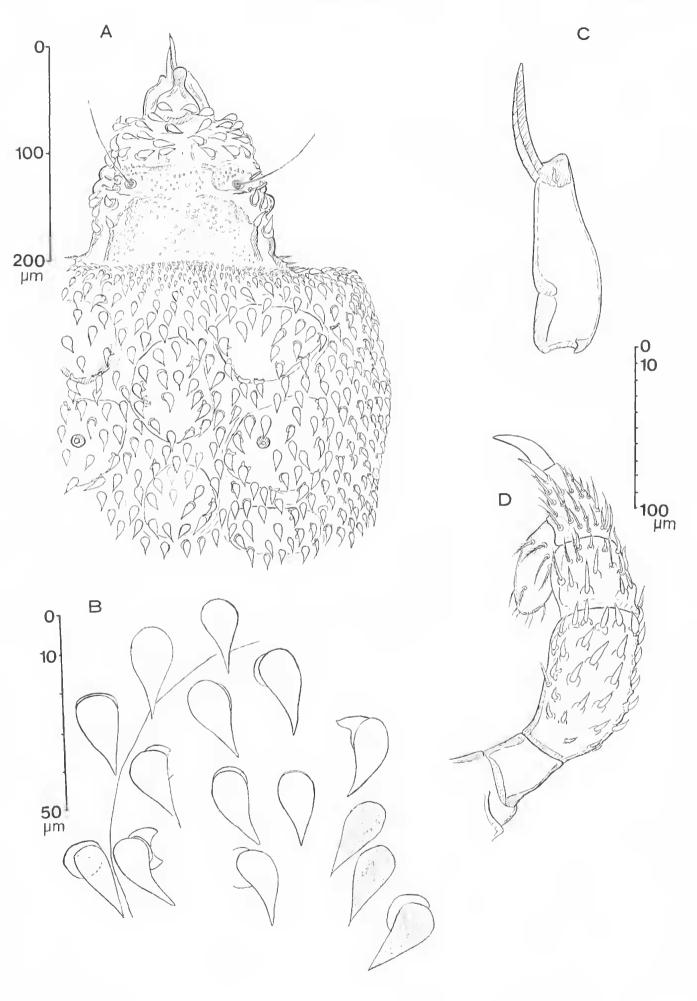
The second, fourth and fifth of lateral row of pits contain, more or less centrally, ring of chitin (appears as "C" in pit 5) set lower than bases of setae; it possibly functions as a respiratory aperture, but could function as muscle insertion; presumably derived from seta base (annulus).

Ventral surface: not clearly seen in ACB712B, but appears to be normal for *Trombella*. Genital aperture

and anus appear to be normal for deutonymphs (somewhat obscured in mounts).

Legs (Figs 6, 8A, B) short, fairly robust for a trombidioid mite, segments beyond trochanters more or less cylindrical. Leg 1 620 long, 11 415, 111 445, 1V 520 (including trochanters to tips of tarsi, without elaws). Each tarsus bearing two claws. All segments of legs with irregular surface due to leg setae (scobalae) originating from small papillae. These leg setae generally robust, and tend to resemble body setae but are much more slender, tapering and blunt-pointed. In more proximal and more distal parts of legs these scobalae tapering, more slender and flexible, more like usual setation of trombidioid mites. Leg segments carrying small spiniform sensory hairs (spinalae) interspersed among scobalae, from telofemora to tibiae.

In leg I (Figs 6, 8A) tarsus from above more or less parallel-sided, 198 long by 67 wide. In leg IV (Fig. 6)



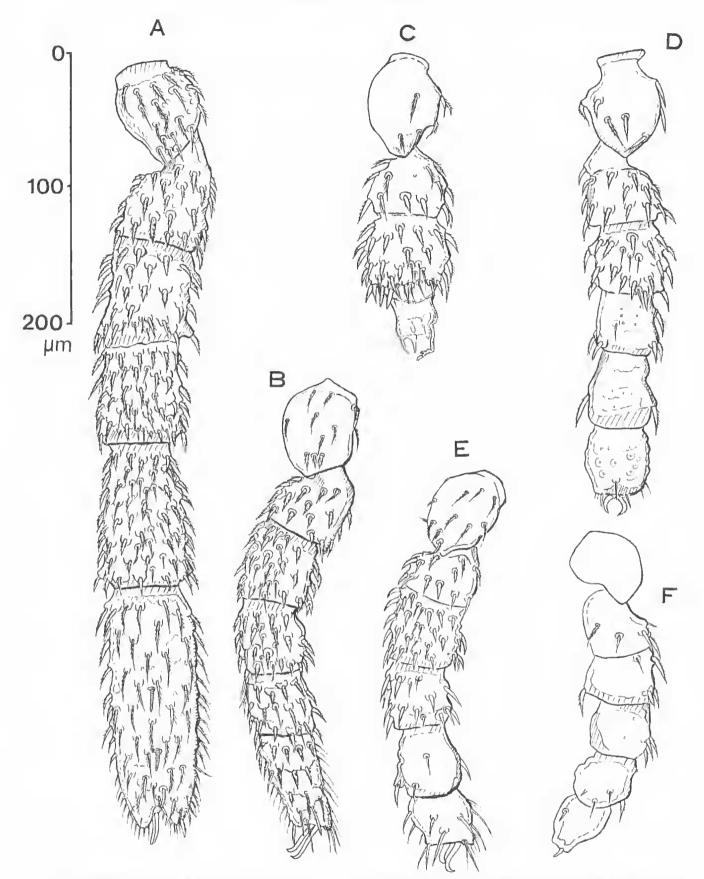


FIG. 8. Trombella alpha sp. nov. Deutonymph. A, B Normal specimen ACB712B, A left leg I, B left leg II. C-F Abnormal legs of specimen ACB712A (see text), C left leg I, showing extensive deformity, with almost complete loss of all segments beyond the telofemur, but all segments somewhat abnormal. D Right leg I, showing a generalized deformity with progressive shortening of segments; note also loss of setae. E Left leg II, similarly affected. F Right leg II, with considerable deformity, including shortening of all segments and gross reduction of setation, and reduction of the paired claws to a single short peg. (All to scale shown.)

FIG. 7. Trombella alpha sp. nov. Deutonymph. A Dorsal view of anterior part of idiosoma and tips of chelicerae, specimen ACB712B. B Further enlargement of the setae of the anterior of the median column of depressions. The surface patterning of three of these setae is shown at the lower right. C Chelicera of specimen ACB712C, D Medial aspect of R palp of ACB712C. (All to nearest scale.)

	Nymphs of					Tromhella ulphu				Adult of T. adelaideae		Adult of T warregensis		
Specimen number	ACB712B		ACB712A* ACB712C		8712C	ACB712D		ACB714B*		ACB729		ACB730		
Segment	μm	ratio	μπι	ratio	μm	ratio	μm	ratio	μm	ratio	μm	ratio	μm	raho
Tarsus I	198	1.00	62	1.00	183	1.00	191	1.00	170	1.00	280	1.00	390	1.00
Tibia I	120	.60	61		106	.58	120	.63	.98	.58	180	.64	320	.82
Genu I	80	.40	49	_79	-1	-	90	.47	-1		148	.53	230	.59
Tarsus IV	126	1.00	122	E.00	135	1.00	133	1.00	125	1.00	214	1.00	311	1.00
Tibia IV	114	.90	113	.93	117	.87	111	.83	105	,84	192	.90	328	1.05
Genu IV	72	.57	73	.60	75	.56	78	.59	72	.58	128	.60	197	.63

TABLE 2. MEASUREMENTS OF LENGTHS (μm) OF LEG SEGMENTS OF A SERIES OF NYMPHS OF *TROMBELLA ALPHA* N. SP.; AND SIMILAR DATA FROM THE HOLOTYPES OF *TROMBELLA ADELAIDEAE* WOM, AND *T. WARREGENSIS* HIRST; TOGETHER WITH RATIOS OF LEG SEGMENTS AS A PROPORTION OF TARSAL LENGTH

\* Teratological specimen. The measurements are taken from the less deformed right side (see text). Legs II and III also show the same deformity (brachymely).

This specimen has a brachymelic right leg III. However legs I and IV appear normal (see text).

Specimen flexed, not measurable in mount.

rarsus tapering, 126 long by 36 wide. For other leg dimensions see Table 2.

Palpi fairly stout, provided with robust scobalae over femur and genu, more distally setae more slender, and some are barbed (see Fig. 7D, from ACB712C). Palpal tibia with strong curved elaw, and accessory claw-like seta on medial side. Palpal tarsus with sparse setation of slender pointed hairs, some barbed.

Cheliceral fang robust, curved, pointed, 71 long, arising from a basis chelicerae about twice as long (Fig. 7C, from ACB712C).

#### Origin of the Specimens of Trombella alpha

This study of Trombella alpha is based upon larvae which have been obtained parasitic upon field crickets, Teleogryllus commodus (Walker), in the New England District of New South Wales, by Mr S. J. Davidson, who commented (pers. comm., 5.xi.1979) on ". . . a redorange coloured mite which appears to be parasitic on gryllids. Up to 50 per cricket have been recorded, with mouthparts attached to the hosts' pleural regions, especially on the metathorax" (see Fig. 3). In a further note (pers. comm., 1982) Mr Davidson has summarized his observations on the parasitisation of the crickets by this mite species as follows: The mite "attaches principally to the soft pleural regions of the host .... Numbers of this mite were monitored by examination of most of the T. commodus trapped in pitfalls from 1979 to 1980. A higher percentage of crickets was parasitised in 1979 than in 1980, with respective means of 61% and 20% .... Similarly, there was a higher mean parasite burden per ericket in 1979 than in 1980. The mite was most prevalent on crickets in about February, and both percentage parasitism and parasite burdens declined in late autumn ....." [Table 3]

# Material examined

ACB711: 4 specimens, collected from paddock number K2, Kirby Rural Research Station, near Armidate, N.S.W., 12.11.1979. Preserved in alcohol, decolorized.

ACB712: 5 specimens, live, crickets collected 12.iii.1980; mites removed 19.iii.1980, (Transformed to nymphs in Adelaide.)

TABLE 3. PERCENTAGE OF T. COMMODUS PARASITISED [BY T. ALPHA] AND THE MEAN PARASITE BURDEN PER CRICKET, OVER TWO SUCCESSIVE SEASONS OF PITFALL TRAPPING AT KIRBY STATION.

Collection date	Number of crickets examined	Percentage of crickets with mite parasites	Mean numbe of mites per cricket		
30.1.79	31	42	0.71		
9.it.79	55	91	7.22		
26.11.79	18	83	8.50		
26.iii.79	79	84	2.80		
9.iv.79	46	50	0.80		
24.jv.79	33	18	0.18		
Mean. (1979)	.44	61	3.4		
11.1.80	119	24	0.34		
8.11.80	14	21	0.36		
7.jii.80	39	1.8	0.23		
4.iv.80	75	15	0.19		
Mean (1980)	62	20	0.3		

Note: These data refer to all instars of the cricket in which the sex can be distinguished, i.e. the last three instars (see also Table 7, and text thereto).

ACB713; Several larvae collected 19.iii.1980; preserved in alcohol.

ACB714: 3 specimens, live, collected 19.iii,1980.

ACB712, ACB713 and ACB714 were all collected 10 km N of Armidale, N.S.W.

Type and paratypes to be deposited in the South Australian Museum.

# Rearing Experiments: Larvae to Nymphs of T. alpha

Deutonymphs were reared from two batches of larvae forwarded to my laboratory, on strips of wet blotting paper in sealed tubes. Experimental details are as follows:

(1) Experiment ACB712. The cricket was collected on 12.iii.1980 and the mites removed on 19.iii.1980. The five larvae sent were received by me on 21.iii.1980. On receipt the mites were immobile, i.e. they were possibly in a pre-pupal condition. One mite was rather swollen, on its back in a film of water on the site of the tube. The legs looked decolorized. One larva was waving its legs about, stuck to glass. The three other larvae immobile, not swollen. Later in the day two mites became immobile and were considered swollen, while two were waving their legs about. All five were stuck in a film of water and the tube was wet.

23.iii.80. All larvae immobile, plump,

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- iii.80. All immobile, not shrivelled, not mouldy. One or more were considered to be in a pre-pupal stage.
- 25-29.in,80. All mites observed daily, and recorded as immobile.
- 30.iii.80. In two specimens "frosting" under the skin of the mite was detected. This was interpreted as representing the development of nymphal setae within the exuviae.
- 31,iii.80. 3.00-3.15 p.m. One larva appeared to be sitting upon a pupa larger than itself. Skin of larva appeared transversely wrinkled. The other larvae were smooth, swollen, not mouldy, and were considered to be in a pupal state.

3.30 p.m. The legs of the nymph were clearly visible. Anterior part of the larval skin had gradually become whiter and more opaque, as though filling with air. A clear gap was visible, most noticeable in the right rear leg.

The legs of the nymph gradually extended away from the body of the animal.

Other larvae also had air under the skin.

- 1.iv.80. Nymphs had not as yet emerged. Two larvac in the tube had prominent protuberances.
- iv.80. Nymphs had still not emerged, despite nymphal palpi and legs being clearly visible within the larval skin.
- 9.iv.80. Camera lucida sketches were made of the transforming larvae (see Figs 4A, B).
- 15.iv.80. Two nymphs had emerged, these being labelled ACB712C and ACB712D. These were not the specimens mainly described above. The cast larval skins of these two mites, also a dead larva (ACB712E), were mounted.
- 16.iv.80. One more nymph (ACB712A) emerged in the morning, and one (ACB712B) at night. The cast skins of these two specimens were mounted.
- 18.iv.80. One nymph (ACB712D) was immobile, possibly dead; mounted. I attempted to feed the nymphs with pieces of apple, culicine mosquito eggs, and squashed adults of *Aedes notoscriptus*, also a sample of bird dung, and the juice of a squashed grasshopper (*Phaulacridium vittatum*), etc. One nymph appeared to feed upon the piece of apple, and possibly feeding could have occurred with the other materials. One nymph (ACB712D) was seen moving slowly as late as 17.v.80; the others had died earlier. Eventually all nymphs were mounted in gum chloral

mountant for study; none had transformed to any later instar.

(2) Experiment ACB714. Three plump larvae were received in wet preparation on 21.iii.80, having been collected on 19.iii.80. All remained immobile, and unaffected by mould filaments spreading slowly across the inner surface of the glass tube, which began to produce spores on 27.iii.80.

On 28.iii.80 one mite was observed to have decolorized legs and mouthparts.

On 31.iii.80 nymphal legs developing in one larva, in its unchanged larval skin, were detected.

On 8.iv.80 one specimen (ACB714A) became mouldy. Another specimen (ACB714C) eventually shrivelled to a more or less spherical object without recognizable features. One larva (ACB714B) was seen to have protruding limb masses by 8.iv.80, and a nymph emerged on 20.iv.80. Food was offered to it in the form of a mass of culicine eggs, pieces of grass, a squashed dipteran, a squashed small weevil, a squashed dipteran, a squashed small weevil, a squashed *Phaulacridium vittatum* etc., and the mite possibly fed. It was not seen moving after 13.v.1980. The mite and its cast skin, and the other larvae used in the experiments, were eventually mounted on slides for study.

From these observations a confident correlation of the larva with the nymph of this species can be made.

Table 4 summarizes the details of the successful larva-nymph transformations.

# Remarks on the Larva to Nymph Transformation

The active nymphal stage of the Parasitengona is currently recognized as the deutonymph. Between the larva and the deutonymph is the protonymph, which, as with most prostigmatic mites in the Parasitengona, is calyptostatic and takes place within the larval skin. In the Erythraeoidea the skin tends to retain its shape when shed by the protonymph, and can commonly be retrieved in one piece after such ecdysis (Frauenfeld 1868; Womersley and Southcott 1941; Southcott 1946a, 1946c, 1961a). In the case of the smaller Trombidioidea the protonymphal skin is thinner and more fragile, so that although there have been many studies on larva to nymphal transformations in the Trombiculidae and other families, rarely is there an attempt to describe the protonymphal stage between the larva and the deutonymph. However, modern exceptions to this statement can be found in the works of Jones (1951,

TABLE 4. DETAILS OF SUCCESSFUL TRANSFORMATIONS OF LARVA TO ACTIVE NYMPH IN TROMBELLA ALPHA N.SP.

Experiment and specimen number	Date collected	Date received	Date became immobile	Date Active nymph emerged	Duration of the immobile phase*
ACB7124	12.iii.80	21.01.80	19-23.111.80	16.iv.80	24-28 days
ACB712B	12.111.80	21.iii.80	19-23.111.80	16.iv.80	24-28
ACB712C	12,101,80	21.111.80	19-23.00.80	15.iv.80	23-27
ACB712D	12.111.80	21 11.80	19-23.111.80	15.iv.80	23-27
ACB714B	19.61.80	21.00.80	19-21 iii.80	20.iv.80	30-32

By subtraction. The figures given express a range of possible dates from the data available. Since there is no precise indication of the time of commencement of the protonymphal stage it is not possible to give any estimate of the duration of that period.

1954), Neal and Barnett (1961), Johnston and Wacker (1967) and Robaux (1974).

An intermediate membrane seen within the investing integuments of the prelarva, or later stages, was named the "Zwischenhaut" by Claparëde (1868) in his study of the development of the water mite Atax bonzi Claparède, the "apoderma" by Henking (1882) in his study of Trombidium fuliginosum Hermann, or the "intermediate skin" by Jones (1951, 1954), in his study on Neotrombicula autumnalis (Shaw). Since deutonymphal development takes place entirely within the expanding larval skin, there appears no need for the protonymph of the Trombidioidea to develop the distinct pupal setation as in the Erythracoidea, and which presumably has a defensive and possibly substrate-anchoring function.

In the case of the developing Trombella alpha deutonymph, some of the successive stages of the gradual transformation from immobile larva through the protonymph to the active deutonymph are shown in Fig. 4A, B. Initially the legs and palpi lose their orange coloration, as the living substance of the animal is withdrawn to a more compact mass. The ventral part of the larva enlarges, so that after several days the appearances are of a larva riding upon a larger rounded structure, a flattened prolate spheroid. The nymphal leg prominences gradually appear, and project increasingly from the main mass. The larval skin appears to separate from the developing nymph, so that the dorsal surface at least appears as whitish and more opaque. The emerging nymph may or may not leave behind a more or less intact larval skin. Generally the "intermediate skin", i.e. the protonymphal skin, remains inside the cast larval skin, so that it is not easy to recognize. Occasionally parts of the protonymphal skin separate from the larval skin, and rarely, the protonymphal skin may appear as a more or less intact structure. Even within the cast larval skin, however, distinct structures may be seen in the exuviae discarded by the nymph. Thus in Fig. 4C there is visible a Y- or T-shaped thickening of the integument ("a"), shown underneath the larval scutum. More posteriorly is a distinct structure, near the midline, which appears as a studded boss or "mateola", with folds of thin skin running up to it ("e" in Fig. 4C). Other less clearly recognizable structures can also be seen, with vague outlines suggesting that they may have been investments of the developing limbs, and sometimes with numerous small elevations (e.g., as shown in Fig. 4C, "b").

One distinct structure is made up of two elongateoval or kidney-shaped valves, surrounded by a large number of small conical elevations in an "area setosa" ('as' in Fig. 5A; see also Fig. 5B). These valves are the same structure as the larval anus or "uroporus", having the same appearance of two apposed valves, but surrounded by a highly modified area of skin. Comparison of the cast larval and protonymphal skins shows that between them they possess only one pair of valves or valve-like structures, which are of the same dimensions as those of the larvae, i.e. these are of larval origin. the area setosa, however, is purely of protonymphal origin. The more or less concentrically arranged elevations are short cones with blunted tips. They are setiform in shape, and either represent precursors to setae, or possibly serve as investing structures for the developing setae of this area of the deutonymph. These protonymphal setae are similar in appearance to the projections of the "studded boss" ("mateola", or small mace) mentioned above.

Although it is not at present possible to allocate anatomical positions or functions to all of the structures of the protonymphal skin, at least some of the main structures can be postulated.

In Fig. 5A is shown a more or less intact protonymphal integument, after slide-mounting through lactophenol and gum chloral media (specimen ACB712A). This is described briefly in the following section,

# Description of Cast Protonymphal Skin (Fig. 5A, B)

This skin (ACB712B) is more or less in one piece, transparent and colourless. Overall length 875, to tip of projecting anterior pointed structure; width 445. General outline oval, with broad rounded posterior end and crumpled but narrower anterior end. Whole of skin with crumpled appearance; only some of the many minor folds are shown in Fig. 5A. The appearance of the skin matches roughly the shape of developing nymph (see Fig. 4B), with widest part and lateral bulges corresponding to legs IV of nymph. The position of anal valves and surrounds corresponds to position of these structures in larva and deutonymph. The anterior part of cast skin is more difficult to assign to corresponding structures, but presumably the various parts are investing integuments to chelicerae, palpi, and the more anterior legs.

The mateola appears in the skin, projecting anteriorly, about midway between the anal area and the front of the skin with folds of integument leading to the base. The "Y-structure" was not certainly identified, but possibly was contained in the folds drawn around the mateola ("m" in Fig. 5A).

Rounded markings present over various parts of cast skin, recognizable as rounded elevations on protonymphal skin. There is no evidence of seta formation in them (such skin elevations are a wellmarked feature of the few developing protonymphs of trombidioid mires that have been described; e.g. Johnston and Wacker, 1967, Fig. 5, p. 307, for *Eutrombicula splendens*).

Several thickened, almost nodular deposits appear within the skin, shown cross-hatched in Fig. 5A, one being labelled " $\pi$ ". Whether these are mere accidental inclusions, or are representative of some consistent process is not known, because only one reasonably intact protonymphal skin was available.

Anal valves (from larva) and area setosa as described above,

Associated with the protonymphal skin in this preparation are only two other pieces of larval skin. One ("ds" in Fig. 5A) consists of the larval dorsal seurum and a small amount of its surrounding skin, detached from the protonymphal skin. The setae of seurum are severely damaged from the processes of transformation, and possibly by the mounting procedure and no seta is intact. The other small larval skin piece is at the posterolateral aspect of the protonymphal skin ('ls' in Fig. 5A).

# Variations in the Leg Structure of the Deutonyinph, and the Developmental Abnormality "Brachymely"

Since dimensions of leg segments are commonly used as species-differentiating characteristics in these and other mites, it is instructive to examine the intraspecific variation of a batch of mites which have been collected from the same area, and handled in the laboratory as uniformly as possible.

Table 2 lists tarsus, tibia and genu lengths of legs 1 and IV of the reared *Trombella* alpha nymphs (also those of holotypes of *T. adelaideae* and *T. warregensis*)).

There is some similarity between ratios of the segmental lengths in the three nymphs ACB712B, ACB712C and ACB714B. However, ACB712A shows gross shortening of the three measured segments of Leg I, but no abnormality in leg IV. This occurs in greater degree distally; and is accompanied by other structural abnormalities. It occurs in legs other than those shown in Table 2, and may vary between the two sides of the animal. This developmental abnormality will be termed "brachymely".

# Brachymely in Trombella alpha and in some other Prostigmatic Mites

Fig. 8C-F shows the deformed legs I and II of ACB712A, compared with the normally developed legs I and II of ACB712B (Fig. 8A, B).

TABL	E 5, COMPAR	ISONS O	FABS	OLUTE	LE	NGTI	IS (µm) OF
	SEGMENTS						
	TROMBELL	A ALPH.	4 NYN	MPHS /	ND	RAT	los

	ACB712A*	ACB712B	ACB712C	ACB714B	m y + z + w	x/m
	λ.	У	2	w	31	
Segment						
Tal	64	198	183	170	183.7	-35
Til	- 61	120	106	98	108	.56
GeI	49	80	-	_	80	.61
TalV	122	126	135	125	128.7	.95
TilV	113	114	117	105	112	1.01
GelV	73	72	75	72	73	1.00

 Measuring the less deformed R leg, for purposes of comparison. In the left leg the segments beyond the femur are unrecognizable from the gross shortening and fusion.
 for 1, in the case of Ge1.

Table 5 shows normal variation for leg 1V in specimen ACB712A; deformities in this specimen are restricted to legs I-III. In the right leg J the tarsus, tibia. and genu are considerably shortened, and the setae much reduced (Fig. 8D). The trochanters, basifemoraand telofemora appear more or less normal, with a minor degree of shortening and some loss of setae in these segments also. The degree of shortening is greater distally. In legs II (Figs. 8E, F) and III there is a reduction of setae throughout the legs, including the two parts of each femur. In right leg 11 (Fig. 8F) and right leg III there is only one tarsal claw to each tarsus. The most extensive deformity occurs in left leg 1, where there is some thickening of the femur, and beyond the femur the remainder of the leg is reduced to a single fused segment (Fig. 8C). In this segment there is no recognizable tarsal claw or claws, with only a rudimentary indication of setae, without any seta basis or other part being distinctly recognizable. (In specimen ACB714B there appears to be a minor degree of shortening of right leg 111, apparently without other abnormalities in the body or other legs. The measurements of the lengths are: Tarsus III 66, tibia 111 76, genu 111 57. In tarsus III and tibia III there is a reduction of setation, and possibly also in genu III. For left leg 111 of the same specimen: tarsus 111 93 long. tibia 111 73, genu 111 58.

There was nothing that occurred in the experimental handling of specimen ACB712A to suggest a reason for the remarkable degree of deformity observed. All of the larvae in experiment ACB712 underwent transformations at about the same time intervals. The abnormalities cannot be attributed to a failure of the production of moulting fluid, as such would simply fail to allow release, but would not be expected to affect limb development. Abnormalities other than in the limb segments were not detected. The cast skin of the larva and protonymph appear normal. The lengths of the leg segments of the larva, also the shield data (see Table 1), are normal. The larval tibiae and tarsi, for example, are normal in structure. The cast protonymphal skin (see Fig. 5A) appears normal. It is the most intact of the protonymphal skins available. for study, at least of those that have separated from the larval skin. It would be inappropriate to attempt to connect some of the parts of the ACB712A protonymphal skin with structural abnormalities of the nymphal legs at the present time, because of the lack of knowledge of the correspondence of nymphal and protonymphal structures.

It is not uncommon for minor abnormalities in leg claw structure to be seen in larval erythraeid mites captured in the field. This has been referred to as "twisted claws" or TC abnormality (Southcott, 1961a, p. 481; 1966, p. 732; 1972, p. 29). More severe deformities are also seen in the legs of larvae caught in the field. Thus in one batch of larvae caught at Imman Valley, South Australia in 1952 many larvae of *Erythrites urrbrae* (Wom.) and *E. reginae* (Hirst) showed a mild tarsal deformity, and one specimen of *E. reginae* showed an extreme deformity of all pedotarsi, which were grossly contracted and distorted (Southcott, 1955).

The cause of these deformities is unknown. An attempt to reproduce them in larval erythraeid mites by chilling batches of eggs resulted in scutal deformities but not leg deformities (Southcott, 1955).

Although it is not unusual for minor abnormalities of scutal structure to occur among prostigmatic mites, involving supernumerary setae or loss of setae (see Southcott, 1966, pp. 756-758), it appears that the limbs of developing mites are more at risk of structural abnormalities (in the form of shortening of segments and loss of setational pattern) than the structures associated with the idiosoma. The claws may suffer a minor deformity, may be grossly distorted, or virtually absent.

Various other developmental abnormalities have been recorded among the Acarina and in other arthropods. Among prostigmatic mites there may be complete absence of a leg, e.g. in the water mite Sperchon glandulosus thienemanni Koenike (Szalay, 1932), or in Eutrombidium otorheiense Feider (Feider, 1946). Simple shortening of a leg, but without other abnormality, has been recorded by Feider (1946) in E. otorheiense, and termed micromely. Schizomely (complete or incomplete duplication of a leg) has been recorded by André (1949, 1960b) in the trombidioid mites Microtrombidium sucidum (L. Koch) and Carpothrombium carduigerum (Berlese). Various leg and other abnormalities in Hydrachnellae and other mites were recorded and discussed by Thor (1926).

Exposure of the developing eggs of other arachnids to supraoptimal temperatures has produced limb, eye and other deformities. Among the limb deformities are brachymely and schizomely (opilionids: Juberthie, 1968; spiders: Jacuński, 1971, Mikulska and Jacuński, 1971, Mikulska, 1973).

The observations reported here indicate that developing limbs of Acarina are sensitive to teratogenic agents, as yet unknown.

#### Classification of Post-larval Trombella

Known post-larval forms of *Trombella* s. str. comprise six closely related species, characterized by the lack of a crista metopica and the presence of large idiosomal depressions, allotted a glandular function by some authors. The genus and species were founded on a single specimen of *T. glandulosa*, found deepty buried in soil, Adria, northern Italy (Berlese, 1887). This specimen, which has not been restudied by any later author, had several unusual morphological features, not recorded for any other species since placed in *Trombella* s. str.; (1) the presence of a chituized pore in *each* of the idiosomal pits, whether dorsal, lateral or ventral; (2) the dorsal idiosomal pits not contiguous,

in fact well separated and occupying only a small proportion of the surface; (3) the posteromost median dorsal pit being set in a group of four of the lateral pits, instead of being set in the midst of a group of six pits; (4) the presence of a long sinuous idiosomal seta arising from a small prominence on the lateral side of each propodosomal sensillum. These features of Berlese's original drawing were reproduced in Thor and Willmann (1947), and the sole further specimen of *T. glandulosa* recorded, from Austria, by Schuster (1960), is stated to correspond accurately in all morphological features they give, apart from being somewhat smaller. One may therefore accept Berlese's drawings as accurate.

The African T. Javosa appears to be the species most separate from T. glandulosa, Dorsally it carries large idiosomal depressions, all lacking a central pore, but surrounded by a prominent ring of chitin. The dorsal idiosomal setae are also markedly different, being in the form of large flattened scales, the scobillum ending in a long central point and being provided with large projections along its lateral edges (André 1936a, 1958). In T. glandulosa the dorsal idiosomal setae are spinelike, simple, and bent near the base of the shaft so that the main part of the shaft is parallel to the surface. In T. lusitanica the general idiosomal setae are spiniform, simple, curved, sharp, on short tubercles (papiltae), only the more peripheral ones of the propodosoma bearing fine setules. In T. warregensis the dorsal idiosomal seta is papillate, clongate, curved near its base, and ornamented with prominent broad setutes in the form of scales or long barbs; in both T. adelaideae and T. alpha the seta presents as a tear-drop perched transversely upon a papilla. In T. adelaideae the scobillum is ornamented with prominent broad scales, while in T. alpha only a reticular pattern is visible (see Figs 7B, 9A-D).

The other hitherto recorded species of adults of *Trombella—T, lusitanica* André, *T. warregensis* Hirst (which appear to be close to each other) and *T. adelaideae* Wom.—differ in having different members of the idiosonal pits with central pores, in setal and leg characters, etc. (One feature used by André in proposing *T. lusitanica* and separating it from *T. glandulosa* and *T. warregensis*, was stated to be its possession of a punctate seta-less area on the propodosoma. However in *T. warregensis* reexamination of the holotype under oil immersion shows minute puncta in this glabrous area. The same glabrous area in *T. adelaideae* and *T. alpha* has small rounded tubereles.)

Thus in *T. adelaideae* and *T. alpha* the dorsal pits carry these chirinous pores or rings more or less centrally in lateral depressions 2, 4 and 5; in *T.* warregensis they are present in lateral depressions 2, 3, 4, 5 and 6; in *T. lusitanica* they are present in lateral depressions 2, 3, 4 and 5 (Andre, 1944).

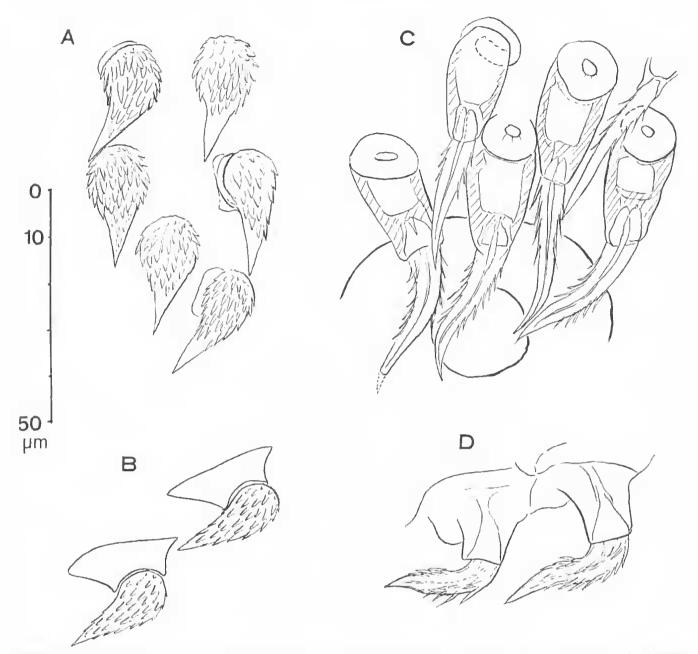


FIG. 9. Dorsal idiosoma setae in adult Trombella. A, B Trombella adelaideae Wom., Holotype, A setae from the anterior median dorsal depression; B setae from the posterolateral edge of the dorsum. C, D T. warregensis Hirst, Holotype, C Group of setae from posterolateral part of dorsal idiosoma; D Two setae in lateral view at the posterolateral edge of the dorsum. (All to scale shown.)

The arrangement of the setae of the dorsal idiosomal pits has been used by authors (e.g. Womersley, 1954b) as taxonomic criteria. Thus the central arcas of these pits in T. favosa bear slender papilla-less spiniform setae (André, 1936a), while in T. lusitanica the pits bear spiniform, conical sctae arising from a short tubercle (Andrć, 1944); in T. glandulosa they are short, conical and curved (figured by Berlese, 1887). In the three Australian species recorded here the setae of the pits do not differ essentially from the general dorsal idiosomal setac. In both T. adelaideae and T. alpha the peripheral setae of the dorsal pits may form a single vague row, but in T. warregensis the central part of the dorsal depressions is nude, with peripherally the setae in one or two fairly regular concentric rows (in T. glandulosa Berlese figures one row of sctac near the centre, and one row at the rim).

Some use has been made of the relative shapes of leg segments and the rations of various segmental lengths as taxonomic characters of trombidioid and other mites, although with soft-bodied mites such as the trombidioids too much reliance should not be placed upon the shape characteristics of the tarsi. For the three Australian species of *Trombella* the ratios of tarsus I length/tibia 1 length and tarsus I length/tarsus I width, are given in Table 6.

The data in Table 6 indicate that *T. adelaideae* and *T. alpha* resemble each other more than either resembles *T. warregensis*, which agrees with the idiosomal seta characteristics.

The data presented or previously published appear adequate to separate species of *Trombella* on a world basis, even though we do not have any species recorded

	ACB712B	Trombella al, ACB712C	ACB712D	ACH714B	T. adel ACI	aideae 1729	T. warregensis ACB730		
<u>Tarsus 1</u> Tihia 1	1.65	1.73	1.59	4.73	1.56		1.22		
Farsal width	67	67	75	65	100µm(L),	10Zpm(k)	176µm(L),	164µm(R)	
Length Tal	2.96	2.73	2.55	2.62	(L) 280	(R) 282	(L.) 390	(R) ca380	
Width Tal					100	102	170	164 2.325	

 TABLE 6.
 COMPARISON OF LEG SHAPE RATIOS IN TROMBELLA FROM AUSTRALIA, USING TARSUS I/TIBIA I, AND

 LENGTH OF TARSUS I/WIDTH OF TARSUS I. IN NYMPHS OF T. ALPHA AND ADULTS OF T. ADELAIDEAE AND

 T. WARREGENSIS (See also Table 5 for figures to lengths)

omitting brachymelic specimen ACB712A. See data in Table 2.

Re-measured from holotype. See data in Table 2. In both leg I is seen in tateral view. Womerstey (1954b, pp. 127, 128) gives these figures as 270 and 90, and the ratio as 3.1. The specimen has not been remounted. (In 1939, p. 149, he gave these figures as 260 and 90.)

§ Womersley (1954b, pp. 126, 128) (who had remounted the specimen) gives these figures as 375 and 135, and the ratio as 2.75:1. Hirst (1929, p. 170) gave 370 and 140, i.e. a ratio of 2.64:1.

in which both adults and deutonymphs have been described. The following key is therefore presented.

# KEY TO THE KNOWN WORLD SPECIES OF POST-LARVAL STAGES OF TROMBELLA S. STR.

- 1. All dorsal pits of idiosoma lack a central chitinized porestructure. Dorsal idiosomal setae flattened, with long median end and 3-5 strong lateral projections. Central areas of dorsal pits with long spiniform setae, not mounted on papillae ..... T. favosa André At least some of the dorsal pits of the idiosoma with
- 2(1) All dorsal idiosomal pits with a central chitinized porcstructure. Dorsal idiosomal setae spiniform, bent near base so that the shaft lies parallel to body surface. Ratio of length tarsus 1/(ibia 1 about 2.0 ... T. glandulosa Berlesc. At least the anteromost of the lateral row of dorsal idiosomal pits lacking a central chifinized pore-structure
- 3(2) Dorsal idiosomal setae long and pointed, the seta scobillum not wider than its basal papilla. Third lateral dorsal depression with central pore-structure ..... 4 Dorsal idiosomal setae tear-drop shaped, the scobillum wider than the basal papilla. Third lateral dorsal
- 4(3) Dorsal idiosomal setae with numerous prominent setules. Chitinized pores present in lateral row pits of dorsum numbers 2, 3, 4, 5 and 6, Tarsus 1/tibia 1 about 1.2. T. wurregensis Hirst Dorsal idiosomal setae either spiniform or with slender setules. Chirinized pores present to lateral row pits of dorsum numbers 2, 3, 4 and 5, Tarsus 1/tibia 1 about
- 5(3) Scobillum of dorsal idiosomal setae with distinct ciliate-Scobillum of dorsal idiosomal setae with smooth surface, not presenting as a ciliate-barbed structure .

### Leg Chaetotaxy of Trombella alpha Larva

Specialized sensory setae upon the legs of larval prostigmatic mites have been of interest to taxonomists for many years, particularly in classification. Although they function as physical and chemical receptors, there have been few functional studies upon them, efforts having been mainly in description and classification, with their functions only rarely being postulated. Classification of these setae has been contentious, with

two main systems being used in the terrestrial Parasitengona, which I have designated the "trombiculid system" and the "Grandjean system" (Southcott, 1961a). Despite these differing classificatory systems, there are no doubts that setal patterns differ. not only between families, but between genera. Within the genera allotted to the family Trombellidae considerable differences in leg setational patterns occur (Southcott, 1982).

Although the presence of modified "normal setae" or scobalae-"mastisetae"-is well-known on the femora of trombiculid mites (Audy, 1954; Southcott, 1961b), the presence of simple sensory setae upon the femora is more restricted. In the Trombellidae, in addition to being present on femur 1, 11 and 111 of Trombella alpha, they were recorded earlier on the telofemora I and III in Ralphaudyna (as nude femoralae) by Vercammen-Grandjean et al. (1974). However, they occur more widely, being also present upon the femur of larval Neotromhidium (Southcott 1954; Borland, 1956) and Monunguis (Lindquist and Vercammen-Grandjean, 1971) (Neotrombidiidae or Neotrombidiinae), in Durenia (Vercammen-Grandjean 1955; Vercammen-Grandjean and Audy, 1959) (Trombellidae) and Hannemunia (Hyland, 1956) (Leeuwenhoekiidae or Leeuwenhoekiinae) and more widely in the Trombidioidea, such as in Megophthrombium (Mullen and Vercammen-Grandjean, 1978) (Microtrombidiinae or Microtrombidiidae), and in various genera of the Johnstonianidae (Newell, 1957; Robaux 1978), It would thus be unwise to place too much stress on the presence of these setae on the femora of the larval instars as a taxonomic character.

Similar smooth sensory setae occur also on the adults and nymphs of Tromhella (Fig. 8A-F). They also occur more widely in the Prostigmata e.g. Smaris cooperi Southcott (Smarididae), referred to as spinalae, spinofemoralae, etc. (Southcott, 1961b), and on genua 1-111 of the nymph of Microtrombidium kirsutum Wom. (Southcott, 1946b),

Another resemblance between Trombella and Ralphaudyna larvae lies in each possessing two palpal femoralae. In Trainhella, however, there are no vestigialae; in *Ralphaudyna* these are present as distinct "mushroom-like microspurs" (Vercammen-Grandjean, *et al.*, 1974, pp. 248-9).

# Generic Classification of the Trombellidae

# 1. Adults and nymphs

Thor (1935) defined the Trombellinae as those Trombidiidae which lacked a crista, with eyes 2 + 2, sessile, setae short and sharp, with two sensory setae. on the propodosoma at the level of the eyes, and some lesser characters, to include only Trombella Berlese. In 1937 Womersley added Chyzeria Canestrini 1897 to be subfamily, as well as Parachyzeria Hirst 1926 (syn. Thaumatothrombium André 1938) (1938b)); this was accepted by Thor and Willmann (1947). However, both Parachyzeria indica Hirst and P. poecilotrichum (André) have two pairs of prosomal sensilla, and therefore should be placed in the family Johnstonianidac Thor 1935, subfamily Johnstonianinae as defined by Newell (1957). Womersley (1954b) described the reared cycless deutonymphs of Audyana Wom., dividing the subfamily into the tribe Chyzeriini for Chyzeria and Parachyzeria, and Trombellini for Trombella, Audvana and Nothrotrombidium Wom., 1954 (erected for the European T. otiorum Berl.), but did not redefine the subfamily. Vercammen-Grandjean (1955) described the reared nymphs of Durenia, and provided a revised key for the tribes and genera of the post-larval Trombellinae. Feider (1955) elevated the Trombellinae to the family Trombellidae, a status which most later authors have accepted (see Southcott 1982). Within this family (or subfamily) two further genera have been proposed for adults or adults and nymphs): Parathrombella André, 1958 and Neonothrothrombidium Robaux, 1968.

In defining these two last-named genera each author stated that a crista metopica is present. In Parathrombella nasuta Andre, the type species of its genus, the propodosoma bears dorsally 1 + 1 eyes laterally, and in the central part there is a thickened chitinous plaque, roughly in the shape of a trapezium, with prominent anterolateral angles, each bearing a sensillary seta, which are thus well separated. There is no anterior linear projection of chitin from this plaque or shield. The hysterosoma bears 10 (or 11) contiguous plates, which resemble those of Trombella, there being four in each lateral row and two or three median. André therefore redefined the Trombellinae, saying that the crista was limited to a more or less developed transverse band, with "rarement un vestige, très reduit, médian". The use of the term crista etc. seems to be largely a matter of terminology. There is no doubt that the two species Andre classified in Parathrombella belong to the Trombellidae. However the other two species that he placed in Parathrombella differ from P. nasuta in having the following three characters: (1) eyes 2 + 2, (2) no large dorsal hysterosomal depressions but instead a hexagonal network connecting the bases of the seta

papillae, (3) two small circular pits anterolaterally on dorsum of bysterosoma. André (1962) recognized that the two latter species come within *Durenia*.

Robaux (1968) erected Neonothrothrombidium, with type species N. franzi Robaux, 1968 from South America, stating that in this genus the crista is well developed, but did not discuss any consequent revision of the definition of the Trombellinae. As earlier (1966) he had referred to a crista in Nothrotrombidium otiorum (Berl.) as consisting of no more than the two prosomal sensillary bosses, he was clearly using the term crista in a wider sense than the majority of authors. Even so, he later (1968) figured in N. franzi a broad chitinous thickening of the dorsum of the propodosoma extending from its rear border, anteriorly enclosing the sensillary bosses and with an anterior gutter-like seta-less delimited extension running into the nasus. In the second species he placed in this genus, N. americanum Robaux, 1968, the propodosoma bears dorsally an oblong plaque, extending only as far forwards as to enclose the sensillary bosses (which are anterior to the eyes), and without any further anterior extension.

In my opinion these large thickened areas on the dorsum of the propodosoma correspond to the dorsal shields of other prostigmatic mites, and could well be termed a scutum rather than a crista. The same situation occurs in *Chyzeria*, where there is evidence of a dorsal propodosomal scutum and also of a rudimentary crista (Southcott, 1982). The crista may be considered as absent in *N. americanum*, and rudimentary in *N. franzi*.

The differences enumerated between *N. franzi* and *N. americanum* justify their generic separation, and for *N. americanum* the genus *Maiputromhella* n. gen. is proposed.

Although the definition of the Trombellinae given by Thor (1935) and Thor and Willmann (1947) included 2 + 2 eyes, yet eyes are absent in *Audyana*, present as 1 + 1 in *Parathrombella*, and as 2 + 2 in *Trombella* and other genera. For *Nothrotrombidium* Wom, the status of the eyes is unclear, as Robaux (1966, Fig. 1D) shows only 1 + 1 for *N. otiorum*, the type species (but does not comment on this in the text), while Andre (1960a) records that *N. brevitarsum* André, 1960, has 2 + 2 eyes.

From the foregoing, a revised definition of the Trombellidae may be offered, with also subfamilies, and a definition of a new genus.

# Family Trombellidae Thor (Originally as Trombellinae Thor, 1935)

Definition: Trombidioidea with absent or rudimentary crista metopica. Eyes absent, or present as 1 + 1 or 2 + 2; if present, sessile. Propodosoma dorsally with a pair of sensilla (trichobothria), set in a fossa which may have an elevated rim, or be present as a papilla with a central hole. Dorsum of propodosoma commonly with a thickened scutum, which may be poorly defined at its borders. Idiosoma commonly highly modified, with pits or depressions with a possible glandular function, and bearing modified setae. Body and leg scobalae borne singly, or in groups upon small cuticular plates.

Type genus Trombella Berlese, 1887.

# KEY TO THE SUBFAMILIES AND GENERA OF ADULTS AND DEUTONYMPHS OF TROMBELLIDAE

- 2(1) Dorsum of hysterosoma with pits or depressions ... 3 Dorsum of hysterosoma without pits or depressions5
- 4(3) Six depressions in lateral dorsal hysterosomal row. Eyes 24–2 Trombella Berlese, 1887 Four depressions in lateral dorsal opisthosomal row. Eyes 1 + 1 Parathrombella André, 1958
- 6(5) Dorsum of propodosoma without significant thickening to a soutum or plaque-like structure. Propodosomal sensilla close together, somewhat posterior to level of eyes (for *N. otiorum* (Berl.), from Robaux, 1966)
   Nothrotrambidium Womersley, 1954
   Dorsum of propodosoma with a well-developed scotum or chitinized plaque in its posteriormedial part. Eyes 2
   + 2

### Definition of a New Genus of Trombellidue

#### Maiputrombella n. gen.

Definition: Trombellidae with 2 + 2 eyes, posterior to level of propodosomal sensilia. Propodosoma hears dorsally a large transverse oblong scutum or plaque, enclosing the sensillary bosses; anterior chitinized extension of propodosomal scutum absent. Body setae short, blunt-ended, on short papillae. Palpal genu bears distally upon its lateral face a row of broadened, spatulate setae. Type species Neonothrothrombidium americanum Robaux, 1968.

This genus is known only from its type species. The generic name is derived from Maipu, Chile, the place of collection, and *Trombella*.

# (2) Larvae

Southcott (1982) discussed the characters of larval Trombellidae, concluding that it was not possible to give a formal definition of a larval trombellid. Of the two subfamilies into which the Trombellidae is here divided, the reared larvae, except *Chyzeria*, belong to the Trombellinae,

A review of the characters of the larval Trombellidae shows that *Womersleyia* Radford has a number of features in common with *Durenia*, so that 1 have decided to restore the former to full generic status (see key below.)

The following is a revised key to the larvae at present allotted to Trombellidae. (*Ralphaudyna* Vercammen-Grandjean *et al.*, 1974, has been included, although a review of its characters, with two pairs of seutal sensilla, shows that its affinities lie with the family Johnstonianidae, near the subfamily Lasseniinae Newell, 1957, where it is provisionally placed.)

# KEY TO THE LARVAE OF TROMBELLIDAE

- Leg segmental formula 7, 7, 7
   Leg segmental formula 7, 6, 6 or 6, 6, 6

7(5) Nasus of sentum small, largely occupied by the bases of the AM scutalae, and with a deep constriction behind Leg tibia 111 with a large solenoidala *Womersleyia* Radford, 1946 Nasus of sentum large, triangular, its lateral borders continuous with anterolateral borders of seutum, with at most only minor constriction. Leg tibia 111 without a large solenoidala

# AUDITORY FUNCTION IN ACARINA

(a) Function of Tarsi in Trombella alpha Larva

The attenuated tarsi of larval *Trombella alpha* represent an unusual shape among larval prostigmatic mites, suggesting that they might serve as sound-receptor organs. If so, they could possibly be useful in locating males of the host cricket. At my request, Mr Davidson, the collector of the specimens and data, has provided information on the numbers of mites parasitic upon male and females of *Teleogryllus commodus*, as well as for sub-adults (A) and A2 instars). As only the adult males stridulate, for the hypothesis to be valid there should be a greater tendency for parasitization of the adult males. In Table 7 data are provided on the numbers of mites on the various instars of the crickets, by date of collection.

Examination of the data in Table 7 shows that there is a greater number of larval mites attached to the adult male crickets than to adult females, the proportion being 3,70/1.15 overall, or greater than 3:1. Submitting the data to a test of the null hypothesis, i.e. that the proportions of the mites on the crickets are independent of sex, we find that  $X^2 = 83.52$  on 1 d. f., i.e., P<.001\*\*\*.

A significantly greater degree of parasitization of the adult male crickets occurs than in the females. It should be pointed out also that as the crickets were captured in pitfall traps (using Vacola jars as traps), there could have been some transfers of mites between the crickets, since these traps functioned over several days and the conditions in the traps the crickets were extremely crowded when many were caught. Although only a proportion of the mites were studied, among the samples submitted there was only this one species of larva.

This finding therefore is consistent with the hypothesis that the mites may find their hosts, at least in part, by the use of a sound-detection mechanism.

Since only the adult male crickets stridulate, the hypothesis may be examined further by comparing the figures of parasitization for the sub-adult crickets; the first and second instar sub-adults are the only sub-adult instars in which the sex is readily determinable. (Mr Davidson advises (pers, comm., 1983) that difficulties in sexing account for some differences between the totals in the tables.)

Table 7 shows that in the sub-adult instars the mites appear to have a preference for the female crickets, with a mean of 1.57 mites per female against a mean of 1.25 mites per male. If however we compare these figures by the same null hypothesis as above, we calculate that  $\chi^2 = 2.90$  on 1 d. f., not significant, i.e. the null hypothesis is not disproved.

There is thus no evidence of a sexual preference by the mites in parasitizing the sub-adult crickets.

These results thus are consistent with the hypothesis that the mites make some use of sound-detection in their searches for their cricket hosts.

#### (b) Possible Auditory Organs in Acarina

It has been suggested above that the larvae of *Trombella alpha* use the leg tarsi as sound-receptor organs for locating the sound-emitting adult males of the crickets, which is supported by the greater incidence of parasitization in adult males than in adult females. Other instars of the crickets are also utilized by the miles (compare Tables 3, 7).

Earlier suggestions have been made that there are structural adaptations in ectoparasitic mites which serve an auditory function in host location. Newell and Vercammen-Grandjean (1964) described two species of mites from Africa in the family Johnstonianidae (Trombidioidea) as *Pteridopus auditor* Newell and Vercammen-Grandjean, 1964, and *P. pseudohannemania* Newell and Vercammen-Grandjean, 1964. *P. auditor* had been collected parasitic upon crickets, while *P. pseudohannemania* was described from a single specimen collected free on the forest floor,

In both of these species there is an unusual morphological arrangement and modification of setae: tarsus 111 and tibia 111 carry a dorsal row of long feathered setae, each of which has a preformed fracture line near its base, corresponding to an interruption of the actinochitin. They proposed that these setae

TABLE 7. INCIDENCE OF TROMBELLA ALPHA ON THE CRICKET TELOGRYLLUS COMMODUS (Only live crickets examined)

Cricket Category Date of Collection	Adult Males			Adult Females			Sub-Adult* Males			Sub-Adult* Females		
	No: of Crickets N <sub>t</sub>	No. of Mites Nm	Nm/Nc	No of Crickets N <sub>c</sub>	No. of Mites N <sub>m</sub>	Nm/Nc	No. of Crickets N <sub>c</sub>	No. of Mites N <sub>m</sub>	Nm/Nc	Crickets N <sub>c</sub>	Mites N <sub>m</sub>	Nm/Ne
30.1.79	6	3	0.5	1	0	0.0	15	7	0.47	ij	12	1.33
9.11.79	10	133	13.3	8	62	7.75	16	87	5.44	20	69	3.45
26.11.79	14	127	9.07	4	26	0.50	0	0	1.1	0	0	-
26.111.79	37	149	4.03	42	72	1.71	0	D.	-	D.	.0	_
9.1.79	18	15	0.83	28	23	0.82	0	0	-	_0	0	1.
24.iv.79	5	1	0.2	.25	5	0.20	î	0	0.0	1	0	0.0
11.1.80	0 -	-0		0	0	_	38	9	0.24	22	13	0.59
8.11,80	5.	:0	0.0	1	0	0.0	7	I	0.14	4	4	1,0
7.11.80	16	8	0.50	11	7	D.18	6	0	0.0	4	1	0.25
4.14.80	10	ĩ	0.1	57	13	0.23	1	.0	0.0	3.	:0	D.01
Totals	118	437	3.70	177	203	1.15	84	104	1.24	63	-99	1.51

\* Adult-1 and adult 2 instars.

subserve an auditory function, allowing the larvae to locate their hosts by a sonar technique. These setae are generally broken off in the older (i.e. fed) larvae. These authors proposed that this row of setae served no further useful function after attachment to the host, (This would be consistent with the general finding that such larvae feed fully on a single host.) Additionally, the tarsi of P. pseudohannemania (but only tarsus III in P. auditor) are highly attenuated, each tarsus ending in a short pedicellus and three claws.

The arrangement of the setae was considered suggestive "of the setae of the antennae of male Culicidae, which are known auditory organs",

In a later paper Vercammen-Grandjean et al. (1965) discussed another form of setal modification in the North American leeuwenhoekiid mite, Whartonia glenni Brennan, 1962, which is an ectoparasite of two species of bats of two families: Phyllostomatidae and Emballuronidae. In this species of mite there are greatly elongated setae ("mastisetae") on the larval tarsus III. These anisotropic setae, identified as mastitarsalae, have two conspicuous bends and points of weakness. Most specimens of setae from mites taken in the field are broken (92.1% of 341 setae), a situation analogous to that seen in the genus Pleridopus. These authors speculate that such setae assist in locating soundemitting vertebrates, such as bats which emit their highpitched sounds even when roosting, when almost all of the opportunities of attachment of these mites can be conceived to occur.

Although these authors do not mention it, some other prostigmatic mites have highly modified setae which might conceivably serve as sound-detecting organs. Thus in the family Erythracidae the general Eatoniana Cambridge, 1898 and Pillophus Berlese, 1916 have such upon the tibia IV of the adults (and possibly also on genu IV). With regard to the possible function of these setae, there termed "plumalae", the author (Southcott, 1961a, p. 486) accepted the views of previous students that these setae were used as sails as a means of progression. It is now apparent that a more detailed study of their function is warranted.

In the case of Trombella alpha larvae, the setational pattern does not suggest that the setae have any possible specialized auditory function. However, the attenuation of all tarsi does suggest that they could function as sound receptor organs in host detection. Such a function might be enhanced by the possession of a single tarsal claw to each leg. The use by this larva of a cricket as its host species is possibly of significance. Since many animals emit sounds for a variety of purposes, such as territory-establishment, echolocation of surroundings and prey, sexual attraction and other functions, it would appear that the development of host-locating organs by their potential parasites is worthy of a wider study.

### ACKNOWLEDGMENTS

I am indebted to Mr Steve J. Davidson, Zoology Department, University of New England, Armidale, New South Wales, for collecting and forwarding both preserved and live larval mites and data for the present study. The South Australian Museum has made available the holotypes of Trombella warregensis Hirst and T. adelaideae Wom., and a paratype of Womersleyia minuta Radford, for study, I thank Mr L. G. Veitch, Principal Research Scientist, CSIRO Division of Mathematics and Statistics, Glen Osmond, South Australia, for aid and advice in statistical matters.

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